

Modelling the future hydroclimatology of the lower Fraser River and its impacts on the spawning migration survival of sockeye salmon

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Abstract

Short episodic high temperature events can be lethal for migrating adult Pacific salmon (*Oncorhynchus* spp.). We downscaled temperatures for the Fraser River, British Columbia to evaluate the impact of climate warming on the frequency of exceeding thermal thresholds associated with salmon migratory success. Alarming, a modest 1.0 °C increase in average summer water temperature over 100 years (1981–2000 to 2081–2100) tripled the number of days per year exceeding critical salmonid thermal thresholds (i.e. 19.0 °C). Refined thresholds for two populations (Gates Creek and Weaver Creek) of sockeye salmon (*Oncorhynchus nerka*) were defined using physiological constraint models based on aerobic scope. While extreme temperatures leading to complete aerobic collapse remained unlikely under our warming scenario, both populations were increasingly forced to migrate upriver at reduced levels of aerobic performance (e.g. in 80% of future simulations, ≥90% of salmon encountered temperatures exceeding population-specific thermal optima for maximum aerobic scope; $T_{opt} = 16.3$ °C for Gates Creek and $T_{opt} = 14.5$ °C for Weaver Creek). Assuming recent changes to river entry timing persist, we also predicted dramatic increases in the probability of freshwater mortality for Weaver Creek salmon due to reductions in aerobic, and general physiological, performance (e.g. in 42% of future simulations ≥50% of Weaver Creek fish exceeded temperature thresholds associated with 0–60% of maximum aerobic scope). Potential for adaptation via directional selection on run-timing was more evident for the Weaver Creek population. Early entry Weaver Creek fish experienced 25% (range: 15–31%) more suboptimal temperatures than late entrants, compared with an 8% difference (range: 0–17%) between early and late Gates Creek fish. Our results emphasize the need to consider daily temperature variability in association with population-specific differences in behaviour and physiological constraints when forecasting impacts of climate change on migratory survival of aquatic species.

Keywords: aerobic scope, Fraser River, *Oncorhynchus nerka*, spawning migration, temperature thresholds

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Introduction

At the global scale, trends in climate change and the associated changes to the hydrologic cycle are well documented (e.g. Loaiciga *et al.*, 1996; Nijssen *et al.*, 2001; IPCC, 2008; Lettenmaier & Su, in press). However, how these global changes will translate to a regional scale and impact animal distributions and fitness is far less certain (Miller & Russell, 1992; Loaiciga *et al.*, 1996;

Morrison *et al.*, 2002). For aquatic species, even modest, localized deviations from ambient norms in water temperature can potentially cause extreme shifts in distribution and productivity (Pörtner & Knust, 2007; Crozier *et al.*, 2008a). In the case of fishes inhabiting the Great Barrier Reef, for example, the margin between lethal temperatures and current summer temperatures is only a few degrees Celsius (Munday *et al.*, 2008; Nilsson *et al.*, 2009). The upper thermal window between temperatures associated with optimal aerobic capacity and a complete loss of aerobic swimming ability in temperate salmon (*Oncorhynchus* spp.) populations is only

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6–7°C (Fry, 1947; Lee *et al.*, 2003), and even moderate increases in temperature may lead to significant reductions in aquatic species ranges (Keleher & Rahel, 1996; Nelitz & Porter, 2009).

Ultimately, how a single population responds to increasing temperature conditions under a warming climate scenario will depend on the collective responses of individuals. Anadromous Pacific salmon are a particularly good model for relating individual-level thermal responses to overall changes in population-productivity because they breed just once in their lifetime and their breeding migration often involves exposure to the highest water temperatures that they may ever experience. Furthermore, Pacific salmon populations living near the southern extent of their range in the Columbia River, Washington and Fraser River, British Columbia have already experienced significant increases in summer freshwater temperatures since the 1950s (Patterson *et al.*, 2007a; Crozier *et al.*, 2008a) and such increases during spawning migrations have been identified as a major threat to the future viability of salmon populations in both the Columbia and Fraser River systems (Rand *et al.*, 2006; Farrell *et al.*, 2008). Indeed, several studies have quantified a negative relationship between episodes of unusually warm river temperatures and salmon health and mortality (Naughton *et al.*, 2005; Young *et al.*, 2006; Patterson *et al.*, 2007a; Crossin *et al.*, 2008; Mathes *et al.*, 2010). As such, improving our understanding of the mechanistic relationships underlying changes in population viability related to regional shifts in water temperature will be crucial for the future conservation of Pacific salmon (Wang & Overgaard, 2007).

A central and underlying feature of mechanistic models relating temperature to fish survival is the recognition that the effect of temperature is a combination of both linear and nonlinear processes (Hinch *et al.*, 2006). The importance of nonlinear thermal sensitivity of fishes was first characterized by Fry (1947, 1957), who introduced the concept of scope for activity (now termed aerobic scope) and showed that the thermal optimum for aerobic scope (T_{opt}) varies among fish species. Aerobic scope is the difference between maximum ($\dot{M}O_{2\text{max}}$) and routine ($\dot{M}O_{2\text{routine}}$) oxygen consumption rates. In the case of salmon, aerobic scope sets how fast a fish can swim aerobically at a given temperature, which is a critical piece of knowledge for modelling the continuous upstream migration of salmonids. Subsequent characterization of these optima points to the generality that thermal sensitivity has likely evolved to be species-specific and population-specific based on adaptation to historically experienced temperatures (Pörtner, 2002; Richter & Kolmes, 2005; Farrell *et al.*, 2008). There is also evidence that a short-

term collapse of aerobic scope when river temperatures near a critical threshold (T_{crit}) in excess of T_{opt} likely reduces the probability of survival (Rodnick *et al.*, 2004; Farrell *et al.*, 2008).

For fish in general, it is well established that extreme temperatures limit energy allocation and aerobic scope (Brett, 1971; Claireaux & Lagardere, 1999; Lefrancois & Claireaux, 2003; Claireaux *et al.*, 2006), which subsequently restricts whole-animal tolerance to thermal extremes (Pörtner, 2002). Consequently, the minimization of aerobic scope at temperatures beyond low and high critical threshold values has already been used to explain climatic impacts on fish distributions in the North Sea (Pörtner & Knust, 2007). Previous studies have also evaluated models forecasting velocity barriers as a function of aerobic cost of transport (Hughes, 2004). Furthermore, reduced thermal tolerance and increased oxidative stress likely begins at temperatures well below T_{crit} (Pörtner, 2002) and such deviations from T_{opt} can be correlated with high incidences of in-river mortality for Fraser River sockeye salmon (Farrell *et al.*, 2008). Consequently, shifts in river temperatures, either through climate change or altered migration behaviour (i.e. river entry timing), can dramatically affect in-river survival of adult salmon as a direct result of changes to their thermal exposure (Cooke *et al.*, 2004; Farrell *et al.*, 2008). On the basis of these results, it has been postulated that forecasting migration success of Pacific salmon using physiological constraint models based on aerobic scope thresholds could potentially differentiate the relative impact of climate change effects among salmon populations (Pörtner & Knust, 2007; Farrell *et al.*, 2008; Pörtner & Farrell, 2008).

In the current study, we simulated species and population-level migratory survival scenarios using a hybrid approach that links output from global circulation models to relevant biological models. More specifically, we chose to focus our efforts on the relationship between future summer water temperature scenarios for the Fraser River Basin and the migratory survival of sockeye salmon (*Oncorhynchus nerka*) in order to exploit the unique combination of data-rich water temperature time series (Patterson *et al.*, 2007a), and the quantified population-specific physiological responses to temperature (Lee *et al.*, 2003) available for this system. We hypothesized that the sensitivity of freshwater migration mortality in response to climate change will vary as a result of population-level differences in migration behaviour (e.g. river entry timing) and physiological constraints relating to critical thermal thresholds for aerobic performance. Our first objective was to produce temperature scenarios at a daily resolution for the Fraser River mainstem using the Goddard Institute for Space Studies global atmosphere–ocean model (GISS

AOM). Our second objective was to develop physiological constraint models relating fine-scale variability in environmental changes to indices of freshwater migration mortality. By tallying the frequency of daily mean temperature exposures exceeding thresholds corresponding to diminishing levels of aerobic scope, we were able to incorporate the importance of short, episodic high temperature events, perhaps lasting only days, that are known to be lethal to migrating adult salmon. We viewed this level of resolution as essential because Fraser River sockeye salmon swim continuously upstream (English *et al.*, 2005; Rand *et al.*, 2006), presumably to ensure arrival at spawning areas for a genetically predetermined spawning date, and so even delays in the order of days could be costly in terms of lifetime fitness.

Materials and methods

Study system

The Fraser River, Canada's largest river to discharge into the Pacific Ocean, has average annual minimum and maximum flows of 1000 and 7000 m³ s⁻¹ and a hydrograph driven by snowmelt runoff in the spring (Foreman *et al.*, 2001). The majority of Fraser River sockeye salmon migrate upstream between June and September (Patterson *et al.*, 2007a). On average, Fraser River sockeye salmon experience a 4-year life cycle. They spend their first 2 years incubating and rearing in freshwater, after which time they migrate as juveniles from their nursery lakes to the marine environment. After 2 years in the ocean, adults return to their natal freshwater spawning grounds.

We focused on Gates Creek and Weaver Creek sockeye salmon populations because relationships between their aerobic scope and temperature are known (Lee *et al.*, 2003). Also, they reflect some of the diversity among Fraser River sockeye

salmon populations in terms of physiological tolerance, river entry and spawning timing and migratory route and difficulty (Table 1). Weaver Creek is also of particular interest because it is one of several sockeye salmon populations to exhibit a recent, dramatic shift in migration behaviour. Before 1995, Weaver Creek salmon delayed in the Strait of Georgia for 4–6 weeks before continuing their upriver migration (Cooke *et al.*, 2004). However, since 1995, a large component of these fish have started to directly enter the Fraser River, causing their peak river entry timing to shift earlier by 4 weeks, from September 29 (pre-1995) to August 29 (post-1995). This behavioural change has resulted in exposure to warmer freshwater temperatures and higher flows than previously encountered, and has been associated with higher in-river mortality (Cooke *et al.*, 2004).

Climate change model

Daily observed river flow and river temperature for the June to September period from 1981 to 2000 were obtained for the Fraser River near Hope, B.C. (~190 km upstream from the discharge to the Pacific Ocean). Observed flows were obtained from Water Survey of Canada, Environment Canada (<http://scitech.pyr.ec.gc.ca/waterweb/formnav.asp?lang=0>) and observed temperatures were provided by the Environmental Watch Program, Fisheries and Oceans Canada (DFO; http://www-sci.pac.dfo-mpo.gc.ca/fwh/index_e.htm; Patterson *et al.*, 2007b).

The basic version of the GISS global coupled atmosphere–ocean–ice model was described in Russell *et al.* (1995). The model used here has a resolution of 3° in latitude and 4° in longitude, with 12 vertical layers in the atmosphere and up to 16 in the ocean. All significant atmospheric gases and aerosols are used to calculate the radiative source term. Freshwater is added directly to the ocean by precipitation and river flow and is removed by evaporation. River discharge is calculated directly as part of the model simulation according to the river routing scheme of Miller *et al.* (1994). River temperature is also calculated directly as part of the model simulation as described in Ferrari *et al.* (2007).

Table 1 Migration characteristics of Gates Creek and Weaver Creek sockeye salmon populations used in this study

	Gates Creek sockeye	Weaver Creek sockeye
In-river migration distance (km)	364	117
Spawning ground elevation (m)	280	10
Median historic river entry date*	2 August	16 September
Historic Hells Gate ambient Fraser River temperature (°C)†	17.8 ± 1.0	14.7 ± 1.2
Historic Hope ambient Fraser River discharge (m ³ s ⁻¹)	4129 ± 949	2177 ± 542
T _{opt} for $\dot{M}O_{2(\text{scope})}$ (°C)‡	16.3	14.3
T _{opt} for $\dot{M}O_{2(\text{max})}$ (°C)	17.5	15.0

*As estimated at the Mission hydroacoustic facility, approximately 70 km upstream of the Fraser River confluence. Averaged over 1977–2008. Because of a recent shift in river entry behaviour for Weaver Creek salmon, their average median date from 1995 to 2008 is 29 August compared with 29 September for 1977–1994.

†Temperature and discharge ranges are presented as median ± SD over a symmetric 31-day period around the median historic migration date for the midpoint of the river migration (Gates Creek = Hells Gate; Weaver Creek = Mission) from 1981 to 2000.

‡T_{opt} for $\dot{M}O_{2(\text{scope})}$ and $\dot{M}O_{2(\text{max})}$ are from Lee *et al.* (2003).

The model's Fraser River basin consists of three grid cells at $3^\circ \times 4^\circ$ resolution. The water fraction of these grid cells is 4%. For each grid cell, the model calculates the mixed-layer depth of the river. The rate of change of mass, M , in this upper layer is given by

$$dM/dt = P + S + R_{in} - E - R_{out} + X, \quad (1)$$

where t is time, P is precipitation, S is the source water runoff into the river, R_{in} is input river flow from the upstream grid cell, E is evaporation, R_{out} is the output river flow from the grid cell and X is mixing of mass from the next lower layer. Source runoff comes from the land component of the same grid cell and consists of both surface and underground components. The change in heat content, H , of the water in the upper layer is given by

$$dH/dt = Q_P + Q_S + Q_{R_{in}} + Q_E + Q_{R_{out}} + Q_X + SW - LW - Q_H, \quad (2)$$

where Q_P , Q_S , $Q_{R_{in}}$, Q_E , $Q_{R_{out}}$ and Q_X are the heat contents transported by the respective processes in Eqn (1), SW is absorbed short-wave radiation, LW is net outgoing long-wave radiation and Q_H is the sensible heat flux. The river mass of a grid cell flows to its downstream neighbour and eventually to the ocean. The temperature of the upper layer of the river is given by $T = H/CpM$ where $Cp = 4185 \text{ J kg}^{-1} \text{ }^\circ\text{C}$ is the specific heat of water.

In the present study, we examined model simulations from 1850 to 2100 and used model river temperatures for the grid cell closest to the observed site at Hope. The simulations include a control with constant 1850 atmospheric composition and a greenhouse gas experiment with observed greenhouse gases and tropospheric sulphate aerosol burden from 1850 to 2003 followed by moderately increasing greenhouse gases based on IPCC (2007) and sulphate scenario to 2100 (<http://aom.giss.nasa.gov/IN/GHGA1B.LP>).

We first assessed the model's ability to simulate daily summer water temperatures in the Fraser River near Hope for a baseline period, namely 1981–2000. This 20-year baseline period was selected to represent variability in historic average summer temperature conditions to which sockeye salmon have presently adapted, given historic river entry timing (Farrell *et al.*, 2008). Validation of the GISS AOM was accomplished by comparing the model's river temperatures from 1 June to 30 September with the matching daily observed maximum, mean and minimum water temperatures. We also compared daily variability in the model output to daily variability in the observed data for the same 20-year period. Distributions of daily modelled and observed temperatures were tested for normality (Kolmogorov–Smirnov test; MINITAB Ver. 13) and equal variance (Levene's test; MINITAB Ver. 13).

The delta, or change-factor method, was applied to the GISS AOM model outputs to adjust for bias in the mean and variability of the climate model forecasts (Diaz-Nieto & Wilby, 2005). The differences (deltas) between daily averages from the baseline and future climate models were calculated and then these deltas were added to the annual daily temperature values from the observed baseline. While the delta method assumes daily variability and autocorrelations remain the same over time, it is a well-recognized and easily applied

approach used in climate impact assessments (Diaz-Nieto & Wilby, 2005).

Salmon impacts

To place future temperature trends in a biologically relevant context, we compared the frequency of exceeding different thresholds known to be critical to salmonid physiology (Bartholow, 2005) for observed baseline and delta-adjusted climate scenarios. We first selected general threshold values associated with literature-reported values of species-level tolerances of 18–21 $^\circ\text{C}$ (see Richter & Kolmes, 2005 review). We then examined more explicit population-specific temperature thresholds corresponding to reductions in aerobic scope for Gates and Weaver Creek populations.

Migratory survival index

The relationship between aerobic scope and temperature was parameterized separately for both Gates and Weaver Creek populations as a function of the difference between $\dot{M}O_{2_{\max}}$ and $\dot{M}O_{2_{\text{routine}}}$ using the best-fit relationships between rates of oxygen consumption and temperature described by Lee *et al.* (2003). Given the large uncertainty with respect to the proportion of aerobic scope that is needed for successful continuous upstream migration, Farrell *et al.* (2008) quantified reductions in migration success associated with warming by introducing 'functional T_{crit} ' values (i.e. thermal thresholds associated with some n percent reduction from maximum aerobic scope). Currently it is not possible to directly quantify migratory mortality associated with a given deviation from maximum scope for three reasons: (a) individual variability within each population in response to thermal stress, (b) uncertainty in the structure and parameterization of aerobic scope-temperature relationships and (c) uncertainty as to the proportion of aerobic scope required for successful upstream migration. We partially resolved these uncertainties in the context of a sensitivity analysis, by examining a range of temperature thresholds (T_{thresh}) associated with 0–100% deviations from maximum scope in 10% intervals for each population. In each scenario, we assumed that a fish encountering a daily temperature exceeding T_{thresh} in the lower mainstem Fraser River could not complete its migration.

For Gates and Weaver Creek sockeye salmon, migration passage through the lower Fraser River is likely the most challenging aspect of their spawning migration because they encounter the highest flows and some of the highest temperatures of their journey (Patterson *et al.*, 2007a,b). At the same time, they have limited opportunity for exploiting thermal refugia because the river is well mixed (Donaldson *et al.*, 2009). For both populations we applied the daily mean temperature as measured near Hope, B.C. as fish passed a single location at the approximate midpoint of their spawning migration (Hells Gate for Gates Creek fish and Mission for Weaver Creek fish). The same temperature data collected near Hope were used for both sites as previous work indicates good agreement among Hells Gate, Hope and Mission temperatures ($<1.0^\circ\text{C}$ difference between these locations; Patterson *et al.*, 2007b).

This approach is similar to that applied by Farrell *et al.* (2008) in reconstructing historic freshwater temperature distributions for Gates and Weaver Creek populations.

We defined a migratory survival index, η , as the proportion of the population experiencing daily temperatures exceeding T_{thresh} at these respective midpoints:

$$\theta_d = \begin{cases} T_d \geq T_{\text{thresh}}; \theta_d = N_d \\ T_d < T_{\text{thresh}}; \theta_d = 0 \end{cases}, \quad (3)$$

$$\eta = \frac{\sum_{d=1}^D \theta_d}{\sum_{d=1}^D N_d}, \quad (4)$$

where d is the day on which fish pass by either Hells Gate (Gates Creek) or Mission (Weaver Creek), T is either the observed or modelled mainstem water temperature, N_d is the number of Gates or Weaver Creek sockeye salmon passing their migration midpoints, respectively, on day d , θ_d is the number of fish encountering temperatures greater than T_{thresh} on day d (either N_d or zero), D is the total length of the run (i.e. the number of days over which fish from a particular population enter the lower river) and η is the proportion of the Gates or Weaver Creek population experiencing temperatures greater than T_{thresh} in a given year (i.e. the migratory survival index). Because water temperatures throughout the lower Fraser mainstem are comparable (Patterson *et al.*, 2007b) and because they likely reflect the warmest temperatures experienced by Gates or Weaver Creek migrants (Hague *et al.*, 2008), we assumed η would be representative of the probability of an individual fish in the population experiencing $T > T_{\text{thresh}}$ along their total freshwater migration. For a given percent deviation from maximum aerobic scope, T_{thresh} was estimated from a cubic spline interpolation fit to the population-specific aerobic scope-temperature curve.

Migration simulation model

Individuals within a population can experience dissimilar Fraser River environmental conditions in a given year as a function of river entry timing (Hague & Patterson, 2007). We simulated some of the uncertainty in the proportion of each population experiencing $T \geq T_{\text{thresh}}$ by randomizing the distribution, timing and length of an incoming run entering the Fraser River (i.e. daily population size frequency distribution) to generate a probability distribution of η values for each population, temperature scenario (baseline or future) and T_{thresh} combination. Run timing distributions were simulated using mixed normal distributions (Holt & Cox, 2008) fit to historic run frequencies for stock-aggregates representative of Gates and Weaver Creek populations (data provided by the Pacific Salmon Commission, Vancouver, BC; Hague & Patterson, 2007). In each simulation, we parameterized the mixed-normal model by bootstrapping from normal distributions for each parameter while maintaining the covariance structure among values. Simultaneously, we bootstrapped from normal distributions fit to historic initial river entry dates (the first date the population was observed in the lower Fraser River at a hydroacoustic detection station near Mission in each year)

and run length (the number of consecutive days over which a population was observed entering the river). The river-entry dates used to simulate Gates and Weaver Creek migration timing were based on years 1977–2008 and 1995 to 2008, respectively. The shorter time period for Weaver Creek reflects their recent change in river entry behaviour. To separate the effects of the shift in river entry behaviour from changes to temperature resulting from climate change, run timing distributions from the same period (1995–2008) were used for both historic and future model simulations for Weaver Creek sockeye salmon under the assumption that their current behavioural patterns will persist into the future.

Simulations were run using both baseline lower river daily summer temperatures for 1981–2000 and delta-adjusted future temperatures from the GISS AOM for 2081–2100. In each simulation we recorded η , the migratory survival index. As described above, sensitivity of η was evaluated using T_{thresh} values associated with 11 different deviations from maximum aerobic scope (0–100% in 10% intervals). We also examined the robustness of our results to the uncertainties associated with river entry timing within each population by comparing the percentage of temperatures exceeding aerobic scope-related thresholds experienced by the first and last 10% of an incoming run distribution, reflecting the current extremes in river entry timing observed for each population.

All simulations were run using R statistical software Ver. 2.8.0 (<http://cran.r-project.org/>).

Results

Climate forecasts

The comparison of observed and modelled daily river temperatures for the two decades in the present climate period (1981–2000) shows that in the early summer (June/July), the climate model generated average daily river temperatures approximately 1.7 °C higher than observed (Fig. 1a). However, in August and September the GISS AOM's temperatures were very close to the observed, with average residuals of 0.4 °C, and well within the measurement error of the original observations (Patterson *et al.*, 2007b). The daily maxima for the modelled 20-year baseline period were very similar to the observed day-of-year maxima (Fig. 1b). However, the model tended to overestimate the day-of-year minima outside of the month of August (Fig. 1c). The observed and modelled temperature variance structures were both normally distributed (Kolmogorov–Smirnov test; $P > 0.05$). The variance of the modelled baseline temperatures was significantly lower than in the observed baseline thermograph (Levene's test $P < 0.05$) for the majority of dates tested, most notably during the mid- and late-summer periods (Fig. 2). However, there was no significant difference in the daily variance of the modelled baseline vs. future-modelled temperatures (Fig. 2).

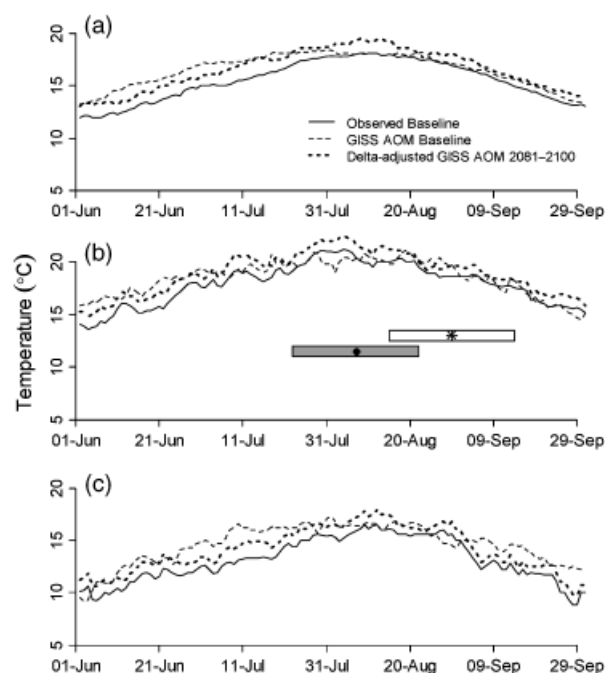


Fig. 1 Comparison of observed baseline (solid line), Goddard Institute for Space Studies global atmosphere–ocean model (GISS AOM) baseline (dashed line), and delta-adjusted GISS AOM 2081–2100 (thick dotted line) 20-year (a) mean and (b) maximum, and (c) minimum 20-year daily summer water temperatures for the lower Fraser River. Average historic migration timing is presented as the median historic midpoint of freshwater migration (Gates Creek = circle; Weaver Creek = star) \pm 15 days (Gates Creek = grey bar; Weaver Creek = white bar).

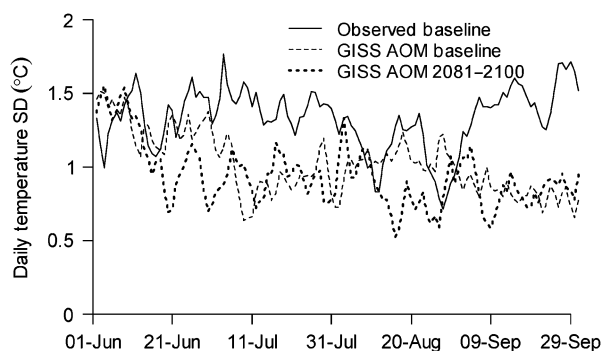


Fig. 2 Comparison of observed baseline (solid line), Goddard Institute for Space Studies global atmosphere–ocean model (GISS AOM) baseline (dashed line) and GISS AOM 2081–2100 (thick dotted line) 20-year daily SDs in summer water temperatures for the lower Fraser River.

The delta-adjusted climate model forecasted that the effect of increasing greenhouse gas concentrations will lead to daily river temperatures increasing, on average, by 1.0 °C by the end of the 21st century compared with

Table 2 The mean (\pm SD) number of days per year where daily lower Fraser River temperatures exceeded critical temperature thresholds (T_{thresh}) identified for Pacific salmon: 18 °C, 19 °C, 20 °C and 21 °C for observed-baseline (1981–2000) and GISS AOM future (2081–2100) scenarios as well as the number of years (out of 20) where each threshold was exceeded at least once

Temperature threshold (°C)	Historic baseline (1981–2000)		Future GISS AOM (2081–2100)	
	Mean days $> T_{\text{thresh}}$ (\pm SD)	# Years T_{thresh} is exceeded	Mean days $> T_{\text{thresh}}$ (\pm SD)	# Years T_{thresh} is exceeded
18	17 \pm 16	20	38 \pm 15	20
19	6 \pm 10	10	17 \pm 15	20
20	2 \pm 5	4	6 \pm 11	11
21	0 \pm 1	1	2 \pm 5	4

GISS AOM, Goddard Institute for Space Studies global atmosphere–ocean model.

the observed baseline (Fig. 1a). Warming trends were most notable during the early and midsummer period with increases in monthly averages ranging from 1.2 °C in June/July to 0.9 °C in August/September compared with observed baselines (Fig. 1a).

Species thresholds

Overall, the average daily temperatures and frequency of extreme temperature events increased when we used the delta method to account for the future changes predicted by the global climate model (Table 2). While the 18 °C-threshold was exceeded in the lower Fraser River at least once in every year from 1981 to 2000 (observed baseline: mean = 17 days/yr, SD = 16), the future climate model forecasted a doubling in the average number of days > 18 °C/yr (mean = 38 days/yr; SD = 15). Historically, water temperatures > 19 °C were observed in 50% of years (mean = 6 days/yr; SD = 10) and were expected to triple in their number of days per year in the future (mean = 17 days/yr; SD = 15). Interestingly, extreme temperatures (> 20 °C) remained relatively uncommon under the future climate scenario. The highest extreme temperature period observed in the Fraser for the 20-year baseline period was a single event consisting of 6 days at > 21 °C in 1998, while the climate model forecasted temperatures > 21 °C to occur once in every 5 years by the end of the 21st century.

Migratory survival index

The delta-adjusted climate model forecasted a 64% overlap in total area between the histograms of

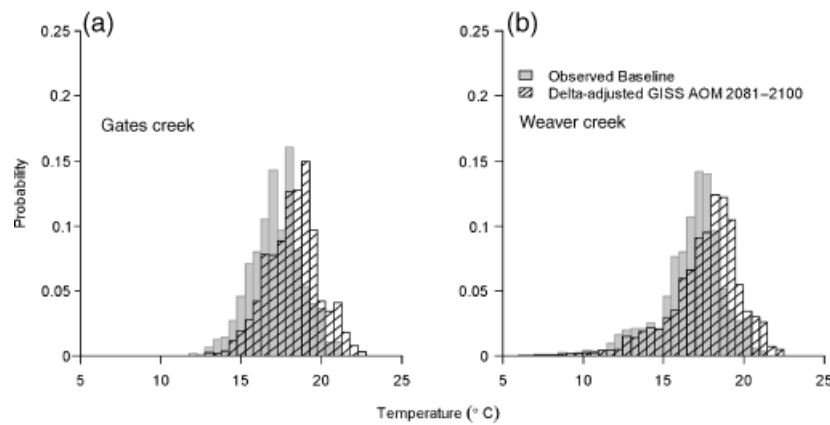


Fig. 3 Histograms of weighted mean lower Fraser River water temperatures experienced by migrating adult (a) Gates Creek and (b) Weaver Creek sockeye salmon under observed-baseline (1981–2000) and Goddard Institute for Space Studies global atmosphere-ocean model (GISS AOM) (2081–2100) scenarios. Weighted by daily run proportions at the midway point of the freshwater migration.

baseline-observed and future-modelled Gates and Weaver Creek temperature exposures (Fig. 3). The median temperature experienced by Gates Creek increased from 17.2 to 18.4 °C, and from 16.9 to 17.8 °C for Weaver Creek. As expected, the forecasted shifts in temperature distributions also translated into a higher probability of Gates Creek and Weaver Creek (Fig. 4) sockeye salmon encountering $T \geq T_{\text{thresh}}$ under future climate conditions.

Figure 4 presents distributions of the proportion of each study population experiencing $T \geq T_{\text{thresh}}$ for deviations ranging from 0% to 100% of maximum aerobic scope in 20% intervals. For the Gates Creek population, temperatures associated with 0–40% deviations of maximum aerobic scope ($T_{\text{thresh}} > 22.2$ °C) were extremely unlikely ($P < 0.005$), even in the warmer river conditions under the climate scenario (Fig. 4a–c). However, for threshold values nearing T_{opt} , there were increases in both the likelihood of a given temperature threshold being exceeded and the proportion of the population affected (Fig. 4d and e). Moreover, the model forecasted an 85% probability that $\geq 90\%$ of the Gates Creek run would encounter Fraser River temperatures above T_{opt} (16.3 °C) under the future climate scenario (Fig. 4f).

In contrast to Gates Creek, 15% of simulations forecasted $\geq 5\%$ of Weaver Creek salmon experiencing temperatures associated with a complete collapse of aerobic scope ($T_{\text{thresh}} = 20.4$ °C); however, the probability of greater than 50% of the run encountering temperatures ≥ 20.4 °C was still only 5% (Fig. 4g). Weaver Creek salmon were also more likely than Gates Creek salmon to experience high temperatures resulting in suboptimal aerobic scope. For example, in 42% of future simulations $\geq 50\%$ of Weaver Creek salmon experienced temperatures associated with $\leq 60\%$ of maxi-

mum aerobic scope, compared with only 5% of simulations for the Gates Creek population. There were also large increases in the likelihood of $\geq 90\%$ of the Weaver Creek population experiencing temperatures above T_{thresh} under the future climate scenario relative to the observed-baseline, [7–21% at 18.2 °C (Fig. 4j); 22–43% at 17.0 °C (Fig. 4k)]. As with Gates Creek, the majority of simulations (82%) predicted that the $\geq 90\%$ Weaver Creek run would experience temperature exposures above T_{opt} (14.5 °C) (Fig. 4l) under the future climate scenario.

The effect of river entry timing on future temperature exposures differed between populations. There was a larger shift in the distribution of temperatures experienced by early (first 10% of the run) vs. late (last 10% of the run) fish for Weaver Creek compared with Gates Creek. Using T_{thresh} values associated with 0–50% deviations from maximum aerobic scope, on average, early entry Gates Creek fish only experienced 8% (range: 0–17%) more $T \geq T_{\text{thresh}}$ than late entry fish. In contrast, early entry Weaver Creek fish experienced 25% (range: 15–31%) more $T \geq T_{\text{thresh}}$ than late entry fish.

Discussion

Climate forecasts

The ability of the GISS AOM to simulate daily summer water temperatures in the Fraser Basin was notable, especially considering that we used a global model simulation with no tuning to account for the specific physical characteristics within a particular basin (Miller *et al.*, 1994; Ferrari *et al.*, 2007). Our confidence in the reliability of the climate forecasts was further strengthened by their consistency with previous climate

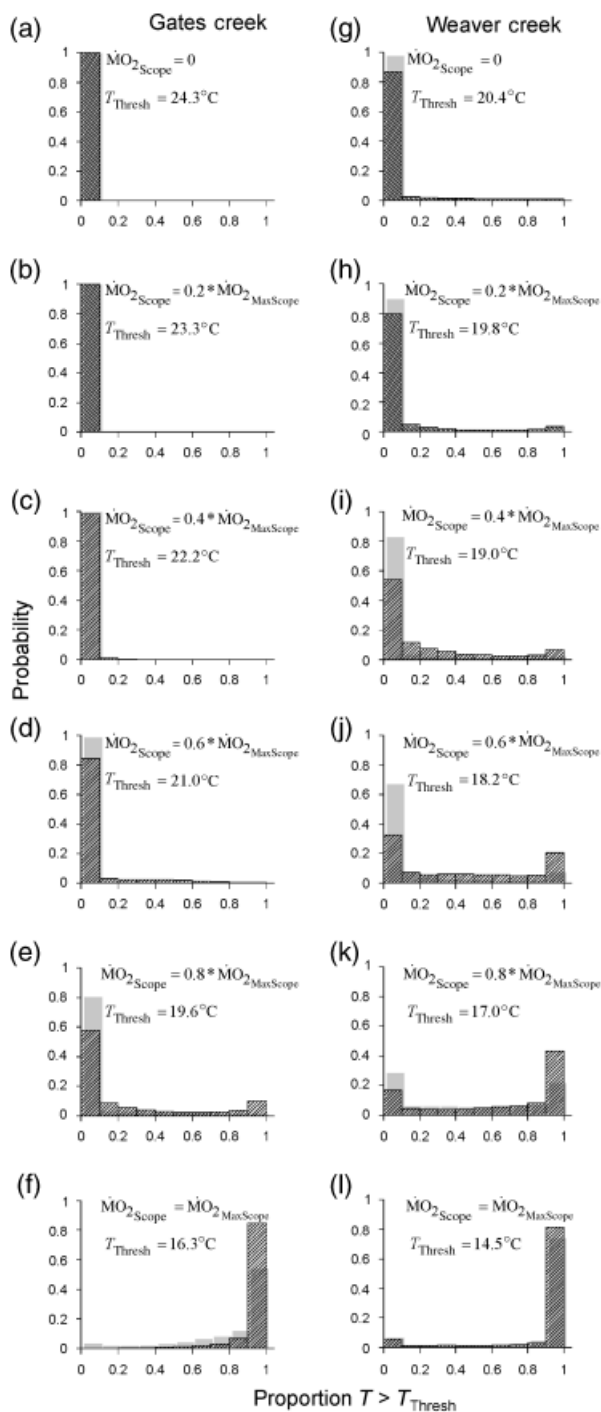


Fig. 4 Probability distributions for the proportion of Gates Creek (a–f) and Weaver Creek (g–l) sockeye salmon experiencing lower Fraser River temperatures exceeding a range of different temperature thresholds (T_{thresh}) associated with percent deviations from maximum aerobic scope under observed baseline (1981–2000; grey bars) and Goddard Institute for Space Studies global atmosphere–ocean model (GISS AOM) (2081–2100; hatched bars) temperature scenarios.

scenarios for the Fraser (Morrison *et al.*, 2002) and Columbia Rivers (Hamlet & Lettenmaier, 1999; Mote *et al.*, 2003; Crozier *et al.*, 2008b). Although downscaling approaches at higher resolution that are specifically tuned for the hydrology of the Fraser River may be less prone to model bias (Morrison *et al.*, 2002), the benefit of the more general downscaling approach applied in the current study is that we provide a tool which is internally self-consistent and can more easily be adapted and applied to other river systems. In addition, these results show that there is promise in the application of downscaling global climate models to similar-sized watersheds that do not have detailed historic temperature or flow records required for developing basin-specific hydrologic models. On the basis of the results in this study, we feel that the GISS AOM does a credible job of recreating summer thermographs for the Fraser River.

At a minimum, validation of the hydrologic component of global climate models should include their ability to accurately recreate historic time series of river temperature (Russell *et al.*, 1995; Morrison *et al.*, 2002; Ferrari *et al.*, 2007) and flow (Miller *et al.*, 1994; Arora *et al.*, 2001; Lucas-Picher *et al.*, 2003). We acknowledge a consistent positive bias in the GISS AOM's baseline daily temperatures in June–July, and an underestimation of daily temperature variability. Possible contributions to this bias could be the climate model's difficulty in accounting for large winter snowpack accumulations and their contribution to early-summer temperature-mediating flows in the Fraser River (Foreman *et al.*, 2001), as well as an accurate forecast of the rate of snowpack melt. Mid- to late-summer river temperatures are more strongly influenced by meteorological conditions such as air temperature and less influenced by snowpack and resulting river flow (Patterson & Hague, 2007). Thus, poor predictability of snowpack could easily produce asymmetry in model bias over the season. Even so, the bias introduced by unpredictably large snowpacks will likely be less pronounced in future simulations because of anticipated shifts towards earlier, lower magnitude snowmelts for the Fraser watershed (Morrison *et al.*, 2002; Stewart *et al.*, 2004; Mote *et al.*, 2005). Other model deficiencies that may affect the accuracy of modelled river temperatures and flow by the GISS AOM are the use of mean volcanic aerosols as opposed to a realistic volcano simulation, a weak El-Niño signal, and frequent light rains in contrast with more infrequent heavier rains that occur in the real world. The climate model's coarse horizontal grid resolution means that future temperature changes and daily variability may be conservative projections because they are averaged over a large spatial area. As model resolution increases, the frequency of high temperature events is likely to increase in some grid cells.

Regardless of fit to observed baseline conditions, caution is still needed when applying future climate model scenarios to forecast population trends. Although the model simulation selected for this study (SRES A1B GHG and sulphate scenario) is considered a moderate scenario, the delta-adjusted temperatures only forecast a rate of change of $\sim 1^\circ\text{C}/100$ years, substantially slower than the historic rate of change observed for mean summer river Fraser River temperatures at Hope between 1950 and 2006 ($\sim 3.3^\circ\text{C}/100$ years; Patterson *et al.*, 2007b) or previously forecasted future rates of change between 1999 and 2099 ($\sim 1.9^\circ\text{C}/100$ years Morrison *et al.*, 2002). Moreover, our forecasts do not account for additional changes in water temperature that may be related to habitat alterations (Nelitz *et al.*, 2007) that could exacerbate the rate of increase. Therefore, the delta-adjusted forecasts used here likely represent a conservative estimate of the actual impact of future increases in greenhouse gas emissions (IPCC, 2007).

Salmon impacts

The results from the future climate scenarios clearly suggest that even a modest increase in mean temperatures corresponds to a dramatic increase in the frequency that critical thresholds will be attained for Fraser River sockeye salmon. As such, climate change is expected to result in significant decreases in the freshwater spawning migration success of certain populations, through increased exposure to both acute and chronic temperature events. The projected increase in the frequency and duration of a threshold exceedence could potentially threaten the future viability of semelparous Pacific salmon populations, particularly those whose life history strategies suggest more limited resilience to changing environmental conditions (Hilborn *et al.*, 2003). These results raise serious conservation and fisheries management concerns under a shifting climate regime. The potential impact on Fraser River sockeye salmon fisheries is particularly evident because forecasts of freshwater mortality indices are already used to directly limit harvest quotas (Macdonald *et al.*, 2010). Improvements to our ability to generate accurate forecasts of salmon freshwater mortality will provide fisheries managers with critical tools for adapting to the impacts of climate change on Pacific salmon.

Our study adopted suggestions from Pörtner & Farrell (2008) and Farrell *et al.* (2008) to provide a novel application of aerobic scope models for forecasting adult salmon migratory survival under future river scenarios. We identified both aerobic scope thermal thresholds and river entry timing behaviour as critical determinants of population-specific responses of Fraser

River sockeye salmon to the effects of climate change. While extreme temperatures leading to complete aerobic collapse remained unlikely for both populations studied, we predicted considerable increases in the probability of large-scale freshwater mortality events (i.e. $\geq 50\%$ of the population) for Weaver Creek salmon due to significant reductions in aerobic scope and associated declines in physiological performance. However, the forecast may not be equally dire across all populations. For example, adult Gates Creek sockeye salmon were less likely to experience a decrease in migratory survival than Weaver Creek fish, despite the fact that both populations were forecasted to experience similar increases in overall temperatures. This result was driven by the population differences in aerobic scope (Lee *et al.*, 2003), likely related to differences in historic temperature exposure (Farrell *et al.*, 2008), and the recent shift in migration timing for Weaver Creek (Cooke *et al.*, 2004). The shift towards earlier river entry timing has increased both the freshwater residency period and exposure to warmer temperatures; as a result Weaver Creek fish already consistently encounter temperatures $> 14.3^\circ\text{C}$ (i.e. their T_{opt}) under the observed-baseline climate scenario.

Ultimately, modelling survival using aerobic scope will depend on the relative difference between T_{opt} and future maximum river temperatures, as well as the temperature sensitivity of aerobic scope. For example, aerobic scope-temperature curves for populations of coho salmon (*Oncorhynchus kisutch*) (Lee *et al.*, 2003) and pink salmon (*Oncorhynchus gorbuscha*) (MacNutt *et al.*, 2006) suggest higher tolerance to increasing temperatures. More broadly, tropical animals are generally considered closer to their upper temperature tolerance than most temperate species (Tewksbury *et al.*, 2008) and may be more likely to experience mortality resulting from a collapse of aerobic scope than temperate fish populations. This variability emphasizes that while the framework and approach to survival modelling presented in the current study could easily be applied across populations, there is still a requirement for further research to parameterize migratory survival models at a population-level.

We chose the collapse of, or decrease in, aerobic scope at daily time intervals as a metric for quantifying the reduction in total migratory survival based on a direct mechanistic link between the diminishment of scope and fish migratory survival (Farrell *et al.*, 2008), and ultimately fitness (Pörtner & Knust, 2007). While thermal challenges associated with diminishment of aerobic scope may not be directly related to survival, they could still impair other physiological systems required to maintain fitness such as disease resistance (Wagner *et al.*, 2005) or reproduction (Patterson *et al.*, 2004), an

area that needs to be explored further. Regardless, future populations of both Gates and Weaver Creek salmon will likely have to endure temperatures that are consistently above their current T_{opt} , causing other physiological challenges and reducing the overall probability of survival until the spawning grounds (Pörtner, 2002; Pörtner & Knust, 2007; Wang & Overgaard, 2007).

The complexity of the true relationship between fish migratory survival and environment involves both acute and chronic effects and cumulative impacts across time and multiple variables (Hinch *et al.*, 2006). Modelling patterns of daily climate variability allows researchers to develop more biologically relevant mortality models which explicitly consider significant migration barriers identified for Pacific salmon (Servizi & Jensen, 1977; Richter & Kolmes, 2005; Keefer *et al.*, 2008b). However, modelling the impact of changes in environment on fish survival involves compromise, with trade-offs between simplified correlational relationships that can break down over time, and more realistic mechanistic models with limited forecasting power and transferability to other systems. Both approaches have been applied to models of Fraser River salmon migration in the past. For example, regression relationships have been used to relate river environmental conditions to salmon migratory survival using indices of spawning escapement (Macdonald *et al.*, 2010) and capture–recapture estimates (Young *et al.*, 2006; Crossin *et al.*, 2008). Alternatively, physiological constraint models have recreated the flow and/or temperature experience along the entire freshwater migration route and then related these profiles to energetic (Rand *et al.*, 2006) or disease (Wagner *et al.*, 2005) thresholds. While our aerobic scope model requires a daily resolution and parameterization of population-specific relationships, it also quantifies a real limitation of temperature on survival of aquatic species. Also, it is easily transferable to studies of other species and systems. As such, we advocate the use of aerobic scope in future migration models for Pacific salmon, and potentially other fish and invertebrate species (Pörtner, 2002).

Our current aerobic scope model is further simplified in that it does not directly model changes in fish behaviour due to selective adaptation. However, the use of a physiological constraint model does facilitate the future exploration of adaptive changes. The capacity for salmon to adapt to the shift in thermal regime is unclear (Henderson *et al.*, 1992), but will likely be a combination of selective pressures, behavioural plasticity, genetics and the rate of adaptation relative to climate change (reviewed in Carlson & Seamons, 2008). For example, some Pacific salmon populations have already demonstrated shifts in river entry timing (Quinn & Adams, 1996; Hodgson *et al.*, 2006; Keefer

et al., 2008a) and/or changes in migratory behaviour to exploit cool water refugia (Goniew *et al.*, 2006; Mathes *et al.*, 2010) in order to avoid extreme river temperatures. Under the evaluated climate scenario, Gates Creek would need to migrate into the river 3 weeks earlier to achieve temperatures near their historic median $T = 17.8^{\circ}\text{C}$ (Table 1). In contrast, Weaver Creek fish would have to migrate, on average, 3 weeks later, to achieve median temperatures near $T = 14.7^{\circ}\text{C}$ (Table 1). To achieve such predictions will require a rate of change in peak timing (21 days over 25 generations) that is almost twice as fast as previously observed rates of change in sockeye salmon (6 days in 11 generations; Quinn & Adams, 1996) and considerably faster than in Chinook salmon (*Oncorhynchus tshawytscha*) (3–5 days in 30 generations; Quinn *et al.*, 2000). Therefore, it seems unlikely Gates and Weaver Creek salmon will be able to fully avoid at least some level of increase in freshwater migratory temperatures over the short-term.

River entry timing is a heritable trait in salmonids (Smoker *et al.*, 1998) and can have a profound influence on in-river survival in migrating adult Fraser River sockeye salmon (Cooke *et al.*, 2004; English *et al.*, 2005). Temperature exposure for Gates Creek was relatively insensitive to shifts in river entry timing within their current range, likely because their normal entry timing coincides with the peak of the Fraser River thermograph (Hague & Patterson, 2007; Patterson *et al.*, 2007a). In contrast, Weaver Creek fish historically enter the Fraser River on the descending limb of the thermograph and so their environmental exposure is more sensitive to changes in run timing (Hague & Patterson, 2007). More interesting perhaps are the implications for directional selection in response to increases in temperature for both populations. For Weaver Creek, the large differential in exposure risk between early and late river entrants may be sufficient to drive heritable changes in migration behaviour (Smoker *et al.*, 1998; Crozier *et al.*, 2008a). The lack of differential risk within the Gates Creek population results in greater uncertainty with respect to potential selection pressures of temperature experience on run timing.

In summary, the present model expands on recent attempts to link future thermal environments to adult salmon migratory survival in two important respects. First, by using daily Fraser River temperatures from a global climate model we were able to assess thermal exposure patterns that are more biologically relevant to anadromous Pacific salmon than patterns that can be assessed using monthly averages. Second, by inserting future river temperature changes obtained from the climate model into physiological constraint models, we removed some of the uncertainty with respect to

the impacts of climate change on aquatic organisms. In doing so, we provide a foundation for developing more complex mechanistic models using aerobic scope which incorporate effects of cumulative environmental impacts, such as combined effects of temperature and flow. This study is a starting point towards making long-range assessments of the thermal regime of the Fraser River Basin under future climate change conditions, and presents one possible method for identifying potential impacts on Pacific salmon through the 21st century.

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